LXIV.—*On the Structure and Classification of the* Asterolepidæ. By R. H. Traquair, M.D., F.R.S.

[Plates XVII. & XVIII.]

Of this remarkable and problematic group of Palæozoic Vertebrata the genera with which I propose to deal in the present communication are *Asterolepis*, Eichwald, *Pterichthys*, Agassiz, *Bothriolepis*, Eichw., and *Microbrachius*, Traq. We shall commence with

Pterichthys, Agassiz, 1840.

(=*Asterolepis*, Pander, pars, non Eichw., non H. Miller.)

The structure of *Pterichthys*, sadly misunderstood by Agassiz, was more satisfactorily discussed by Egerton (8); but the writer who in former times knew most about it was Hugh Miller. It is, indeed, strange that though Miller published in 1841 (3) wonderfully accurate figures both of its upper and under surfaces, Agassiz should have mistaken the belly for the back and should have given in his "Old Red" such an utterly bizarre and incorrect restoration, which has, moreover, been copied and recopied into so many text-books, down even to the present day.

A brief account of *Pterichthys* was given by M'Coy in his 'Palæozoic Fossils,' in which Hugh Miller's ideas as to the number and arrangement of the plates of the carapace are corroborated. No attempt is, however, made to go into the structure of the pectoral appendages, while as to the head he says that it is "covered by several irregular polygonal pieces, the exact form of which is still doubtful." The fin observable on the tail was regarded by M'Coy as an anal (6, p. 598 *et seq.*).

Pander, in his classical 'Placodermen' (7), has given some figures of Scottish examples of *Pterichthys*, which, however, do not help us much with those details not already known. But assuming that *Asterolepis*, Eichwald, and *Pterichthys*, Agassiz, are synonymous terms, he added to his elaborate and valuable restoration of the Russian *Asterolepis ornatus* a tail and dorsal fin taken from the Scottish *Pterichthys* (pl. v. fig. 10); and I must agree with Lahusen (11) in protesting against this figure having been reproduced in various works not only as "*Pterichthys*" but even as one or other of the species of *Pterichthys* occurring in Scotland *.

* For instance as "*Pterichthys Milleri*" in Owen's 'Palæontology' (1860), p. 121, as "*Pterichthys cornutus*" in Prestwich's 'Geology' (1888), vol. ii. p. 80.

There is therefore abundant reason for going afresh into the anatomy of the organisms discovered by Hugh Miller, Malcolmson, and Stables, and named by Agassiz *Pterichthys*. The special structure of the head and limbs was hitherto almost unknown, and there is also room for rectification as regards the body-carapace and tail. And this investigation is also of great systematic importance as bearing on the question as to whether Pander was right in maintaining the identity of Agassiz's genus with Eichwald's *Asterolepis*; for as "*Asterolepis*" has the priority, the only ground for maintaining *Pterichthys*, were Pander right in his contention, would be the inadequacy of Eichwald's original description of *Asterolepis*, and then that name would have to be cancelled, as it cannot legitimately be applied to the great Coccostean, named *Homosteus* by Asmuss, and familiarly known to us as Hugh Miller's "*Asterolepis* of Stromness." With that question is also bound up that of the distinction of *Bothriolepis*, Eichwald, a genus also considered by Pander to be synonymous with *Asterolepis*; for although Lahusen (11) and Trautschold (12) have given good reasons for retaining it as valid, the latest writer on the subject, Whiteaves, treats the question as one concerning which certainty has not yet been attained (15).

Head.—The cephalic shield of *Pterichthys* (Pl. XVII. fig. 1) is of a semicircular or, rather, semielliptical shape, rounded in front and truncated behind, where it joins the body-carapace. In the centre it shows a transverse opening, distinctly represented in Hugh Miller's early drawing (3, pl. i. fig. 1), and which, though it was not mentioned by Agassiz, is nevertheless indicated in his figures both of *Pterichthys testudinarius* (4, tab. iv. fig. 2) and *Pamphractus hydrophilus* (*ib.* tab. iv. fig. 6 and tab. vi. fig. 2). This opening, slightly contracted in the middle and expanded on each side, I shall simply call the *median opening*, though it has usually been regarded as an "orbit," and more recently Cope has put forward the view that it represents the mouth in the Tunicata (17). It is entirely filled up by a small plate or system of plates rarely seen in *Pterichthys*, but, as we shall see further on, well displayed in many specimens of the allied genus *Bothriolepis*. The nuchal region is occupied by a plate, the *median occipital* (*m. o.*) shaped somewhat like the conventional royal "crown," but without the pinnacle in the centre. Marginally it shows six aspects or articulations—one posterior, straight, articulating with the median dorsal plate of the carapace; two lateral, each of which passes first forwards and then obliquely forwards and outwards, articulating with the lateral occipital

(*l. o.*); two antero-lateral, passing at an angle forwards and inwards, articulating with the lateral plate on each side; and one anterior, retracted in the centre, so as to form a wide reentering angle in which the correspondingly angulated posterior aspect of the postmedian plate (*p. m.*) is received. On each side of the median occipital is the *lateral occipital* (*l. o.*), of an irregularly pentagonal shape and having one side internal, articulating with the median occipital; two posterior, articulating with the anterior dorso-lateral (*a. d. l.*) of the carapace; one anterior, articulating with the lateral plate of the head; and one external, joined to the *angular* (*ag.*). The latter (postmarginal, Owen) is a very small plate, also forming part of the cranial shield behind the lateral plate. In front of the median occipital, which it entirely separates from the median opening, is a transversely elongated plate, the *postmedian* (*pt. m.*), broadest in the middle, narrow at each end. Its gently convex anterior margin forms the posterior boundary of the median opening; its posterior margin, obtusely angulated, fills up the reentering angle of the front of the median occipital, while each narrow extremity or outer margin articulates with the lateral cranial plate.

Each *lateral plate* (*l.*) is of an antero-posteriorly elongated form and may be described as having four margins. The very irregular inner one articulates with the median occipital and postmedian, is then notched to form the outer margin of the median opening, in front of which it articulates with the *premedian* (*p. m.*); the outer margin, slightly concave, articulates with *extralateral* (*e. l.*), the posterior with the external occipital, while the short anterior one forms part of the front margin of the cranial shield.

The remaining plate (*e. l.*) of the cranial shield is that which in *Asterolepis* has been named "opercular" by Pander, "marginal" by Owen; but I prefer to call it *extralateral*. Forming the lateral margin of the buckler external to the lateral plate on each side, this element attains a large size in *Pterichthys*, and seems to have been only loosely articulated to the side of the head, as it so frequently occurs dislocated and removed from its position, while the other cranial plates still cohere together. In fig. 4 I have represented it in an isolated condition, where it will be seen that its inner margin, which must have been largely overlapped by the lateral plate, shows a peculiar notch a little in front of the middle. (Compare Pander's figure of the same plate in *Asterolepis* (7, tab. vi. fig. 1, no. 3).)

I have seen no trace in *Pterichthys* of the narrow plate which Pander figured in *Asterolepis* (7, tab. vi. fig. 1, no. 2)

under the name of "os terminale," as forming the anterior margin of the cranial shield in front of the premedian and right and left laterals. This bone Pander admitted he had never found perfect in the Old Red Sandstone of Livonia, but thought that he found it *in situ* in Scottish examples of *Pterichthys* (*ib.* tab. vi. fig. 5). Nevertheless on comparing the figure here quoted with numerous examples of *Pterichthys* I am satisfied that the suture there indicated as marking off the "os terminale" is only the transverse groove, belonging to the lateral line system, which crosses the front part of the head.

Of the small, narrow, doubly curved ossicle designated by Pander "Oberkiefer" (7, tab. vi. fig. 1, no. 1) I know nothing; but the oblong plates which he named "Unterkinnlade" or "maxilla inferior" are preserved *in situ* in numerous examples of the Scottish *Pterichthys*. This supposed lower jaw (*mn.* Pl. XVII. fig. 2) consists of two somewhat narrow oblong plates, meeting each other in the middle line and placed transversely on the under surface of the head right in front of the semilunar plates (*s. l.*) of the ventral body-carapace. Each is narrower at the outer than at the inner end and somewhat concave above; frequently they occur displaced forwards, even to a position altogether in front of the head. These plates may indeed have formed the inferior (or posterior) boundary of the mouth; but it is clear that their mode of working must have been rather different from that of the mandible of ordinary Vertebrata.

Before leaving the head of *Pterichthys* it may be well to point out the distribution of the lateral line system on this part. In all the Asterolepidæ, as well as in the Coccosteidæ, this system consists of grooves, which are apt to be, and have often been, mistaken for sutures, actual or obsolete; but they do not occur on the inferior surfaces of the bones, and their connexion with a similar groove running along each side of the body amply demonstrates their true nature. In *Pterichthys* each cephalic groove (Pl. XVII. figs. 1 and 2, represented by the double dotted lines) passes from the dorsolateral plate of the body on to the external occipital, where it at once bifurcates, a transverse branch passing across over the posterior part of the median occipital to join its fellow of the opposite side. The main groove then runs forward on the lateral cranial plate, and, arriving in front of the median opening, it bends inwards to join the opposite groove on the premedian plate, on which it forms a small backward flexure. This course is altogether similar to that in *Asterolepis*; but, as we shall see, it is in some particulars different from the arrangement seen in *Bothriolepis*.

Body-carapace.—This, as already shown by Sir Philip Egerton and Hugh Miller, is nearly quite flat below, high and vaulted above, the sides rising at right angles to the base; as the former author says, "the contour must have had considerable resemblance to a high-backed tortoise with the carapace culminating near the anterior margin," the transverse section being "not unlike the outline of a stirrup-iron." It is composed altogether of thirteen plates, being two more than the number given by Hugh Miller, but agreeing in this respect with *Asterolepis* as described by Pander.

The general form of these plates is already so well known from the descriptions of Hugh Miller and Egerton that I need here only allude to certain matters of detail which require correction, some of them, however, being of considerable importance. In Pl. XVII. figs. 1, 2, and 3, I have represented the outlines of the body-plates as seen from the back, belly, and side respectively, the thick black lines representing overlapping edges, as seen on the external surface, the thin ones those which are overlapped, and which consequently are concealed externally when the plates are *in situ*.

The first point of importance is the presence of two small narrow plates (*s. l.* fig. 2), each of which occupies a space cut out from the inner half of the anterior margin of the anterior ventro-lateral (*a. v. l.*) and is in contact mesially with its fellow of the opposite side. This is Pander's *semilunar* in *Asterolepis* (7, pl. vi. fig. 1), and though not mentioned in the descriptions of Hugh Miller and Sir Philip Egerton, the space which it occupied is distinctly seen in one of Sir Philip's figures (8, p. 305, fig. 2).

Next, as to the anterior ventro-lateral plate itself and the mode of articulation of the arms. Notwithstanding the contrary opinion of Hugh Miller and M'Coy, Sir Philip Egerton strongly maintained that the arms were articulated to separate "thoracic" plates, marked off by a distinct line of suture from the anterior ventro-lateral; and so confident was he in this opinion that he went so far as to say that he was "at a loss to conceive how Professor Pander can have been led to assign the attachment of the arms to the ventro-lateral plates as shown in the magnified figure on tab. vi. of his magnificent work on the Devonian fishes, although in the preceding plate these organs are correctly drawn as appended to the thoracic plate" (9, p. 105). Now in this matter Pander's accuracy cannot be impugned as far as *Asterolepis* is concerned, for the Russian plates of this genus were found isolated and uncompressed, and the place of articulation of the arm can easily be verified on a specimen of the anterior

ventro-lateral plate of *A. ornatus* in the British-Museum collection. And as regards Sir Philip's appeal to Pander's figures 5 and 9 on tab. v. of his work, in which the "thoracic" plates seem to be represented in specimens of *Pterichthys* from Lethen, he could not surely have read the author's explanation of these figures, in which it is expressly stated that this appearance is due to fracture!

Nevertheless, accepting Pander's description of these parts to hold good for *Asterolepis* and Egerton's for *Pterichthys*, Beyrich (10), Lahusen (11), and Zittel (16) have sought herein to find a diagnostic mark between the two genera; but this idea I cannot corroborate. Careful study of a large series of Scottish examples of *Pterichthys* has convinced me beyond all doubt that Egerton was in error on this point and that his "thoracic" plates are simply parts of the anterior ventro-laterals, separated not by a *suture*, but by an internally projecting ridge, which, in crushed and decorticated specimens, gives the false impression of a division. I may add that the species *macrocephalus*, in connexion with which Sir Philip expressed his opinion so strongly, is not a *Pterichthys*, but a *Bothriolepis*, and that isolated plates of the larger species of the same genus demonstrate absolutely the unity of the anterior ventro-lateral and the position upon *it* of the pectoral articulation.

The articular fossa on the outer side of the anterior ventro-lateral in *Pterichthys*, with its contained helmet-process grasped by the articular plates of the arm, and the foramen for the passage of the vessels and nerves to the same, seems to be conformed exactly as in *Asterolepis*; and as these parts have been so well described by Pander from Russian specimens of the latter genus, it is needless at present to enter into detail respecting them. If the Scottish and Russian genera are distinct the diagnosis must be founded on something else than the articulation of the limbs.

Thirdly, as to the articulation of the body-plates with each other. Sir Philip Egerton states that "all the plates of the carapace, with the exception of the lozenge-shaped plate *g* (of the under surface), are united by simple sutures; this, on the contrary, is attached to its neighbours by broad squamous sutures, the lateral bones overlapping its margins on all sides" (8, p. 306); but in the same paper he quotes Hugh Miller to the effect that the two median dorsal plates overlapped some neighbouring ones and were themselves overlapped by others. Now my observations show that all the plates of the carapace were connected with each other by overlapping or squamous sutures, a marginal band along the internal surface of the

overlapping plate being thinned off to fit on to a corresponding band along the margin of the outer surface of the one overlapped. The hexagonal *anterior dorsal plate* (*a. d.*) in this way overlaps the anterior dorso-laterals, but is itself overlapped along its postero-lateral margins by the posterior dorso-laterals, and also behind by the posterior median dorsal, though in this latter case the contrary is stated by Hugh Miller (*ib.* p. 309).

The *anterior dorso-lateral* (*a. d. l.*) overlaps the posterior dorso-lateral, but is itself overlapped by the anterior median dorsal and by the anterior ventro-lateral.

The *posterior dorso-lateral* (*p. d. l.*) overlaps the anterior median dorsal, but is itself overlapped by all the other plates with which it is in contact, viz. the posterior median dorsal, the anterior dorso-lateral, and the anterior and posterior ventro-laterals.

The anterior ventro-lateral overlaps the anterior and posterior dorso-laterals, the posterior ventro-lateral, and the median ventral, while the right one overlaps its fellow of the opposite side in the mesial line.

The posterior ventro-lateral overlaps the median ventral and the posterior dorso-lateral, but is in turn overlapped by the anterior ventro-lateral. In the middle line the plate of the left side overlaps its fellow.

The Arms.—These are comparatively short, as in *Asterolepis*, and I find their structure to be essentially similar to those in that genus as described and figured by Pander. They are hollow, divided by a transverse joint into two segments, proximal and distal, rather flattened above and below, especially towards the extremities, and composed of numerous plates, which have much the same contour above and below. In the proximal segment (Pl. XVII. figs. 1 and 2) we have the following plates:—two *articular* (*ar*), dorsal and ventral, which grasp the helmet-process of the anterior ventro-lateral plate; one *internal articular*, only visible from the inner side of the limb, and therefore not shown in the figures; one *external marginal* (*m*), extending nearly along the whole of the outer aspect of the segment; one shorter, *internal marginal*, and two *anconeal*, or elbow-pieces (*a*), dorsal and ventral, somewhat triangular in shape, their apices directed forwards to meet the posterior extremities of the articulars, their convexly rounded bases articulating with the central plates of the distal segment. The distal segment or "forearm" consists of two *centrals* (*c*), dorsal and ventral, rhombic in shape, with the acute angles truncated, one acutely pointed *terminal* (*t*), and four *marginals* (*m*), of which two follow each other

on the outer aspect, and two are similarly placed on the inner aspect of the limb.

The Tail.—In most Scottish examples of *Pterichthys* more or less perfect remains occur of a tail, covered with small rounded or somewhat hexagonal, slightly imbricating scales, which are arranged in longitudinal rows and also in transverse bands, the scales of one band alternating with those of the next; on the dorsal aspect close behind the carapace is also a small fin (Pl. XVII. fig. 3). Along the dorsal margin the scales are different in shape from those on the sides; in front of the fin they seem to be in the form of a few narrow, longitudinal, median plates; behind it they are elongated and imbricating, the arrangement reminding us of the so-called fulcra or V-scales along the extremity of the tail of an Acipenseroid fish; but whether they are monostichous or distichous it is hard to determine. The external sculpture of the scales is rarely seen, and can therefore hardly be available as a specific character. (See Agassiz's figure of the scales of *Pt. cornutus* in 4, pl. ii. fig. 3.)

The *fin* is triangular-acuminate in shape and seems to have been covered with small scales, no distinct rays being seen. At least two specially prominent elongated scales are placed along its anterior margin, producing an appearance which has been mistaken for that of a spine. The position of this fin is undoubtedly *dorsal*, as held by Hugh Miller, and not anal, as supposed by M'Coy (6, p. 599). Sir Philip Egerton supposed that in addition to the dorsal two ventrals were also present (9 *a*, p. 127); but having examined the specimen, now in the British Museum, on which he founded this conclusion, I find that the two supposed ventrals are merely parts of the dorsal separated by a little fault or dislocation in the stone.

As regards the British species of *Pterichthys* I have already indicated my views in the 'Geological Magazine' of last month. Their characters, so far as I can see, are entirely dependent on slight differences in the shape of the carapace and of the terminal segment of the arm, so that I have often suspected that after all only one "good" species was really represented. Were this view to be adopted, then the name *Pterichthys Milleri*, Ag., would include all the others as varieties.

Asterolepis, Eichwald (published April 1840).

(= *Asterolepis*, Agassiz, pars, non Hugh Miller; *Pterichthys*, Owen, Whiteaves, et cet. auct. pars, non Agassiz.)

We have seen that Pander maintained the identity of

Asterolepis, Eichwald, with *Pterichthys*, Agassiz; and as the priority lay with *Asterolepis*, he proposed to abolish the latter name altogether, as being a mere synonym. We have also seen that the attempt to base a generic distinction on a supposed difference in the mode of articulation of the arms cannot hold good, as Egerton's "thoracic" plates exist no more in the one case than in the other.

There is certainly a very remarkable resemblance in the form and arrangement of the plates of the head and of the arms, though as regards the former I must make a few remarks. I have never in *Pterichthys* found any trace of the "*os terminale*" figured by Pander in his restoration of *Asterolepis*, and concerning which he admitted that he had never found it perfect in the Old Red Sandstone of Livonia; yet its existence in the Russian form seems probable enough if, as described by Pander, the anterior margin of the premedian shows a sutural surface indicating the apposition of another plate in front of it. I have seen nothing like the "*os dubium*" in *Pterichthys*, though it may be the central part of an arrangement like that which closes up the "orbit" in *Bothriolepis*. Lastly, although there is in *Pterichthys* an "angular" element in the same position as that shown in Pander's figure of *Asterolepis*, it does not seem to project backwards in the same way from the margin of the cephalic shield.

As the plates of the Russian *Asterolepis* have hitherto been found only in a disjointed condition, it is natural that no tail should have occurred in apposition with the body; Pander has, however, referred to the dermal covering of this part certain curious bodies found in the Old Red of Russia, and with which he considered the fragments known as *Psammolepis*, Ag., *Cheirolepis splendens* and *unilateralis*, Eichw., *Microlepis exilis* and *lepidus*, Eichw., and *Ctenacanthus serrulatus*, Ag., to be identical. I have never had the opportunity of examining any of these bodies, and can only say that, judging from Pander's descriptions and figures, there does not seem to me to be any reason for connecting them with *Asterolepis*, especially as he himself admitted that they differ in structure from the body-plates, being composed of vaso-dentine, while the latter are composed of true bone. It is therefore clear that no comparison can be instituted between *Pterichthys* and *Asterolepis* so far as the tail is concerned.

There remains the body-carapace. This is more depressed than in *Pterichthys*, but the number and general arrangement of the plates are the same. As regards their mode of articulation Pander does not enter into any great detail either in

his figures or text; but he makes one important statement regarding the anterior median dorsal which demands attention, namely that its lateral margins have on the underside narrow squamous surfaces which overlap both the anterior and posterior dorso-laterals ("unter welche sich die beiden seitlichen Schilder 12 und 13 unterschieben"), a statement borne out also by his figures of the plates in question. Now we have seen that in *Pterichthys* the anterior median dorsal plate does not overlap the posterior dorso-lateral, but is certainly overlapped by it, so that we have in this circumstance a quite tangible mark of distinction between the two genera.

I have not seen the anterior dorso-median plate of *Asterolepis ornatus*; but in the Upper Old Red Sandstone of Nairnshire remains of a large Asterolepid are not uncommon in which this plate certainly had the same relations to the surrounding ones as Pander has described in the Russian form. This is the *Coccosteus maximus* of Agassiz (4, p. 137, tab. xxx *a*. figs. 17 and 18), who supposed the plate in question was a median ventral, while Hugh Miller, with a better conception of its real nature, wished to consider it the dorsal plate of "*Pterichthys*" *major*. Having now got together a very instructive set of its plates, I find that this creature is not *Pterichthys major*, which is in reality a *Bothriolepis*, but a species closely resembling the *Pterichthys* of the lower beds in all essential respects save its depressed form and the mode of articulation of its anterior median dorsal plate. In Pl. XVIII. figs. 1 and 2, I have given outlines of the upper and lower aspects of this plate, the articular surfaces being shaded by horizontal lines. There it will be observed that on the outer aspect (fig. 1) there is no articular surface but the one, *z*, at the posterior margin which is overlapped by the posterior median dorsal, while on the under surface (fig. 2) the antero- and postero-lateral margins show each a narrow surface, *x* and *y*, which overlap the anterior and posterior dorso-laterals respectively. Isolated specimens of the dorso-lateral plates show corresponding surfaces on their outer aspects. The rest of the creature, as I have said, resembles *Pterichthys*, but the carapace is more depressed, the anterior and posterior dorso-lateral plates being narrower. The limbs are short and are similar in construction to those of the last-named genus; and though I have seen little of the head, what I have seen appears to correspond. As regards the tail, as no really entire specimen of the creature has occurred, it is difficult to speculate; but numerous rounded scale-like bodies occurring in the same beds may possibly be referable to this part.

I therefore propose to refer this species to *Asterolepis* under

the name of *A. maximus*, Ag., sp., the name being fortunately suited to its large size, as median dorsal plates sometimes attain a length of 6 inches.

Bothriolepis, Eichwald, 1840.

(*Pamphractus*, Agassiz; *Homothorax*, Ag.; *Asterolepis*, Pander, pars; *Pterichthys*, Ag. et cet. auct. pars; *Bothriolepis*, Ag., pars.)

Bothriolepis was founded by Eichwald upon certain plates or fragments of plates occurring in the Old Red Sandstone of Russia which differed from those of *Asterolepis* in having the surface pitted instead of tuberculated. From his very brief original description (1) it is evident that he had before him fragments of a creature allied to *Pterichthys*; but unfortunately he ascribed teeth to it and imagined its scutes to be arranged in longitudinal rows, like those of the sturgeons, with a rough shagreened skin or smooth enamelled scales between them. By Agassiz *Bothriolepis* was placed among the "Cœlacanthi," and though the plates figured by him as *B. ornatus*, Eichw., are Asterolepid (or Pterichthyid) in character, he gave the name of *Bothriolepis favosus* to an undoubted Rhizodont. In establishing the family of Placodermata to include the Cephalaspidæ of Agassiz except *Cephalaspis*, M'Coy (5) rightly included *Bothriolepis*, and Pander went so far as to assign to it a place among the synonyms of *Asterolepis*, Eichw., along with *Pterichthys*, Ag., and many other names.

However, the dorsal plate figured later on by Eichwald (2, pl. lvi. fig. 3) as belonging to his *B. ornatus* not only stamps it as Asterolepid, but leads us also to suspect that it is generically different both from *Asterolepis* and *Pterichthys*, and that this is the case was clearly shown by Lahusen (11). Describing a head with a portion of the body attached, as well as the two median dorsal plates and some other fragments of the body and arms of a species to which he gave the name of *B. Panderi*, Lahusen pointed out, first that the course of the cephalic furrows (lateral line system) was not the same as in *Asterolepis*; second, that the postmedian plate was different in shape; third, that there was no *os terminale*; fourth, that the articular plates of the arms were longer. But when he speaks of the arms being more simple in structure than those of *Asterolepis* and we compare his figures, it is quite clear that he had before him only the proximal segment of the limb; and it must also be noted that in some cases he regards the grooves of the cephalic lateral line system as sutures, or at least as former sutures, and so very considerably increases the number of bones which he allots to the cranial shield.

Trautschold's contribution to the structure of *Bothriolepis*, published shortly afterwards (12), consists largely of corrections of Lahusen's paper in matters of detail. He also formulates the differences between the heads of *Bothriolepis* and *Asterolepis*, laying stress on much the same points as Lahusen, but adding that the angular and opercular elements (Pander) found in the latter are wanting in the former genus, though, strangely enough, the angular is represented in the diagram which he gives of the head in *Bothriolepis*. Noteworthy it is that he mentions having found in one specimen a lid or cover to the "orbit," and accurately fitting it. As regards the arms, of which he had no complete specimens, he pointed out certain differences in the arrangement of their constituent plates and considers it doubtful whether the limb was divided into proximal and distal portions, as in *Asterolepis*.

The discovery by the officers of the Canadian Geological Survey of numerous well-preserved entire specimens of *Bothriolepis* in the Upper Devonian rocks of Scaumenac Bay enabled Mr. Whiteaves to give a description (13, 14, 15), accompanied by excellent figures, of a new species of the genus, to which he gave the name of *Pterichthys* (*Bothriolepis*) *canadensis*. These specimens are certainly the finest examples of Asterolepid remains yet discovered, and clearly show all the salient features of *Bothriolepis* in a manner never before exhibited. Unfortunately Mr. Whiteaves does not seem to have had complete access to the literature of the subject, as he makes no reference to the papers of Egerton and Beyrich on *Pterichthys* or to those of Lahusen and Trautschold on *Bothriolepis*, and consequently does not seem to be aware that the identity of *Asterolepis*, Eichwald and Pander, and *Pterichthys*, Agassiz, had ever been questioned, or that very tangible differences between *Bothriolepis* and *Asterolepis* had been already pointed out; for as regards the former he says, "It is still open to question, however, whether the genus *Bothriolepis* is or is not a valid one, and sufficiently distinct from *Pterichthys*" (15, p. 106).

However, he bases his reference of the Canadian species to *Bothriolepis* on the sculpture of the plates, pointing out some discrepancies in the plates of the head compared with those in Pander's restoration of "*Pterichthys*" (=*Asterolepis*); and noticing the absence of a tail, he contents himself with saying "It seems therefore highly probable that *Bothriolepis* will prove to be distinct from *Pterichthys* proper." Even as regards the species he seems to be in doubt as to whether or not it is distinct from *B. ornatus* of Eichwald.

But if the generic distinctions between *Asterolepis* and

Pterichthys are but slight, nothing can be more salient than those which distinguish *Bothriolepis* from both, as will be seen from the following sketch.

Head.—The median occipital (*m.occ.* Pl. XVIII. fig. 6) has its lateral margins more perpendicular to the posterior one, the anterior margin shows not merely a shallow reentering angle for the postmedian plate, but a deep semielliptical notch or excavation. The postmedian is small, narrow, semielliptical in shape, and, except its anterior margin, is entirely received in the aforesaid notch of the median occipital, not extending on each side to join the laterals, as in *Pterichthys* and *Asterolepis*. The laterals (*l.*) are much broader, while the extra-laterals (*e. l.*, B in Whiteaves's figure) are very small and narrow; but I have not seen the still smaller plate which Whiteaves figures as A in front of the last-named.

The pattern of the cephalic lateral-line grooves is considerably different from that in *Asterolepis* and *Pterichthys*. No transverse commissure unites the lateral groove of each side across the occipital plates, as in those genera; but in front, just at its inward flexure on the lateral plate, a conspicuous branch is given off which runs forwards and outwards to the margin of the shield, while immediately behind the origin of this branch and on the inner side of the main groove a small car-shaped mark is often, though not always, seen. On the median occipital two slighter grooves are seen, forming an angle with each other behind, whence, diverging obliquely forwards and outwards, they pass also over the lateral plates and terminate near the flexure of the great groove, close behind the origin of its small outer branch.

These grooves are only superficial and have nothing to do with sutures, either present or former; nevertheless their having been considered as such has, as in the case of *Coccosteus*, given rise to confusion in the enumeration of the plates of the cranial shield. Owing to this source of fallacy, Whiteaves, like Lahusen, has numbered, in his figure of the head of *B. canadensis*, no less than seven plates more than what really exist, namely his no. 2 in front and on each side his nos. 2 *a*, 3, and 9 *a*, though he owns that 9 *a* "may possibly be a part of the postlateral" (external occipital). That is undoubtedly the case, and in like manner 2 *a* and 3 are portions of his prelateral (lateral) and 2 of the premedian. Nos. 2 and 2 *a* he regards as equal to the "*os terminale*" in *Asterolepis*; but if we turn to Pander's figure (7, tab. vi. fig. 1) we shall find that similar divisions are marked off by a similar groove on the premedian and lateral plates altogether independently of the division between these plates and the *os terminale*.

The median or "orbital" opening is in perfect specimens of the head of *Bothriolepis* filled up by a system of plates, being the "Decke" already noted by Trautschold. Whiteaves describes the arrangement as consisting of four elements, one central, like Pander's "*os dubium*," one anterior, and two lateral, of a rounded form, stating besides that the anterior one shows a remarkable slender process passing from the middle of its anterior surface right down through the head. I have not seen these plates in *B. canadensis*, but the "lid" is well shown in two specimens of *B. hydrophilus* in the Edinburgh Museum, in which the rounded lateral parts are seen to be very convex above. I cannot in these specimens trace any separation into distinct plates; but this may be due to mode of preservation.

Whether this median opening represents morphologically the mouth of the Tunicata, as Prof. Cope has suggested (17,18), or not, the lateral convexities of the lid distinctly indicate that it covered a paired organ or pair of organs; and what paired organs could we more readily suppose to occupy this position than the eyes? But of what use could the eyes be if covered above by an opaque bony roof? Here I would venture a suggestion. May not the slender descending process described by Whiteaves be for the attachment of muscles arising from the inner aspect of the shield, which, on contraction, would elevate the entire lid above the level of the surrounding cranial plates, and enable the eyes to see out from below its margins? I do not put forward this theory with any notion of infallibility, but it does seem to me more consistent with the actual arrangement of the parts than that which supposes the median opening to be a mouth, the position of which was, I think, more probably on the under surface of the front of the head.

On the under surface of the head Whiteaves figures two plates (13, pl. vii. fig. 1, no. 15), of which he says that they "no doubt correspond to the plates which Pander calls the lower maxillæ." Except that their anterior margins come too far forwards, these plates do remind us of the pair seen in *Pterichthys* immediately in front of the semilunars, and which Pander in *Asterolepis* has interpreted as "Unterkiefer." Is it not possible that the exceeding closeness of their anterior margins to the edge of the cranial shield in Whiteaves's figure may be due to a slight forward displacement, such as often occurs in *Pterichthys* to a much greater extent? In a specimen of *B. canadensis* in the Edinburgh Museum remains of these plates occur, which evidently are so displaced, as they are shoved forwards quite over the edge of the cranial shield.

I have not seen the small median plate which Whiteaves (same figure, no. 18) represents immediately behind the two last mentioned, and concerning which he remarks, "Judging by analogies with the *Asterolepis* of Hugh Miller, but not of Pander, this may have been the hyoid plate." Unfortunately for this comparison, the "hyoid" plate of Hugh Miller's *Asterolepis* (=*Homosteus*) was, thirty years ago, determined to be the *median dorsal* plate of its carapace (7, p. 76).

Body-carapace.—This is more depressed in *Bothriolepis* than in *Pterichthys*, has a dorso-lateral angulated margin as well as a ventro-lateral one, and the dorsal surface is broader than the ventral one. The median dorsal plates are not so acutely elevated mesially as in *Pterichthys*; in some species they are only gently convex on the upper aspect. The anterior median dorsal, usually rather wide in its shape, articulates as in *Pterichthys* (but not as in *Asterolepis*), its antero-lateral margin overlapping the anterior dorso-lateral, while the postero-lateral margin is, on the other hand, overlapped by the posterior dorso-lateral. The inner surface of this anterior median dorsal (Pl. XVIII. fig. 3) shows a sharp median ridge, from which anteriorly two short branches are seen to diverge at acute angles forwards and outwards. On the inferior surface of the body the anterior ventro-laterals (Pl. XVIII. fig. 5) show a peculiarity in shape which distinguishes them from the corresponding plates in *Pterichthys* and *Asterolepis* in not exhibiting in front the prominent emargination for the semilunar plates seen in those genera. In fact no precisely similar semilunar plates exist, though these seem to be represented by a single small triangular one occupying the median notch at the union of the two anterior ventro-laterals. This is figured by Whiteaves in *B. canadensis* (*tab. et fig. cit.* no. 17), and it is indicated, though obscurely, in many specimens of *B. hydrophilus* (Pl. XVIII. fig. 5).

The lateral-line groove is continued on the body-carapace from the external occipital along the dorso-lateral plates on each side immediately below their longitudinal flexure. In addition to this another groove in the form of an inverted V is seen on the dorsal surface, the apex of the V being a little in front of the middle of the anterior median dorsal plate, while its legs extend outwards and backwards over the posterior dorso-lateral (see Pl. XVIII. fig. 4).

Arms.—The pectoral limbs in *Bothriolepis* are distinguished from those of both *Pterichthys* and *Asterolepis* by their greater length, which usually equals or even exceeds that of the carapace, and this is due chiefly to the greater

proportional extent of the proximal segment of each. Consequently the articular and marginal plates of that segment are of greater length than in those two genera; but what is more remarkable is that the anconeal element (Pl. XVIII. fig. 4, *a*) is reduced to a small rounded plate on the dorsal, and apparently entirely wanting on the ventral aspect of the limb; so that beyond the articulars the marginals are entirely in contact with each other on the ventral side, and only separated towards their extremities on the dorsal. In so far as the proximal joint is concerned the limb of *Bothriolepis* may be said to be simpler in construction than in *Pterichthys*; but this is not true of the distal part, in which both the central and marginal rows contain each at least one additional plate.

Tail.—It is remarkable that no tail is seen in *Bothriolepis*, although numerous specimens both of *B. canadensis* and *B. hydrophilus* seem perfect in every other respect. It is therefore perfectly plain that caudal scales were absent, though it does not seem to me quite so safe to assume that no caudal appendage was ever present; for the posterior aspect of the carapace shows a large opening just as in *Pterichthys*, out of which it is difficult to conceive that absolutely no body-prolongation ever proceeded, and it does seem quite possible that a tail might have existed, though unprovided with hard parts capable of preservation. Moreover, in a specimen of *B. canadensis* in the Edinburgh Museum there is to be seen, just at the place where the tail occurs in *Pterichthys*, a peculiar dark organic-looking film, which is strikingly suggestive of the remains of such an appendage.

British Species of Bothriolepis.

B. hydrophilus, Ag. sp. (=*Pamphractus hydrophilus* and *Andersoni*, Ag.; *Homothorax Flemingii*, Ag.; *Pterichthys hydrophilus*, Miller, Egerton).—This interesting form, remarkable for its occurrence in great numbers crowded together in the Dura-Den fish-bed, was elevated by Agassiz into a genus distinct from *Pterichthys*, but on mistaken grounds, as he compared what was in reality the *ventral* surface of that genus with the *dorsal* one of the present subject. The error of this diagnosis having been seen by Hugh Miller and Sir Philip Egerton, *hydrophilus* was restored by them to *Pterichthys*, to which, indeed, Agassiz himself had first of all referred it.

Recently, however, on carefully developing the specimens on a portion of Dr. Anderson's original slab, now in the Edinburgh Museum, I was interested to find that this species

does not belong to *Pterichthys* after all, but is an unmistakable *Bothriolepis*, closely allied to *B. canadensis*. This is at once apparent from the restored figure of its upper surface which I have given on Pl. XVIII. fig. 4. It differs somewhat in the sculpture of the plates, which is delicately pitted-reticulate, while in *B. canadensis* it retains rather more of a confluent tubercular character over most parts of the carapace. The proximal joint of the arm seems also slightly longer in proportion to the distal, and the denticulation of its outer margin rather coarser.

It is quite obvious that, as Hugh Miller and Sir P. Egerton have already pointed out (8, pp. 311 and 314), *Homothorax Flemingii*, Ag. (4, tab. xxxi. fig. 6), is founded on a bad drawing of the under surface of the species under consideration.

B. major, Ag. sp. (=*Pterichthys major*, Ag.; *Placothorax paradoxus*, Ag.).—This has been already referred to *Bothriolepis* by Lahusen (11), whose opinion I can amply corroborate. Its remains, as they occur at Scat Craig, near Elgin, are very fragmentary; but I think they are identifiable with those which occur at Heads of Ayr in a more perfect state. Tubercles of the surface confluent, sometimes into tortuous ridges, more generally forming a reticulation, the stellation of their bases often observable; limbs with the proximal joint proportionally long and slender.

B. macrocephalus, Egert. sp. (=*Pterichthys macrocephalus*, Egert.).—The long arms and the shape of the anterior parts of the ventro-lateral plates clearly show that this minute species is a *Bothriolepis* and very closely allied to *B. hydrophilus*, Ag. sp. This is quite evident from a glance at Sir Philip Egerton's figures (9); but I have also carefully examined the type specimens in the British Museum. The body-plates are sculptured with a delicate reticulate pitting also resembling that of *B. hydrophilus*.

In the 'Geological Magazine' for last month (November) I have named and briefly defined two additional species, viz. *B. giganteus*, Traq., from the Upper Old Red of Alves, near Elgin, and *B. obesus*, Traq., from a similar horizon near Jedburgh.

Microbrachius, Traquair, 1888.

(=*Pterichthys*, pars, C. W. Peach; *Microbrachius*, Traq., Geol. Mag. Nov. 1888.)

The small species discovered by the late Mr. C. W. Peach in the Lower Old Red of John o' Groats, and named by

him *Pterichthys Dickii**, shows some peculiarities which seem to me to be decidedly of generic value.

It is small in size, head and carapace together measuring only about $1\frac{1}{4}$ inch in length. In shape it resembles *Bothriolepis*, having the carapace generally depressed and broader on the upper than on the under surface. On the upper surface the anterior margin of the carapace forms a deep reentering angle (see Pl. XVIII. fig. 8) or emargination, so that the antero-external angles of the anterior dorso-lateral plates project considerably in front.

The anterior dorso-median is peculiarly broad in shape. Its antero-lateral margin on each side first envelops the anterior dorso-lateral, and is then overlapped by it, this relation of the plates to each other being thus suddenly reversed. Behind this the postero-lateral and posterior margins of the plate are, as in *Pterichthys* and *Bothriolepis*, overlapped by the posterior dorso-lateral and the posterior dorso-median; the last-mentioned plate shows posteriorly a prominent angular point, projecting over the hinder opening of the carapace. On the underside the median ventral plate is extremely small. The arms are short, slender, and pointed; the plates of the head, which is large, are not well enough preserved to be readable. The outer surface of the body-plates is minutely tuberculated, the tubercles often tending to confluence in concentric lines.

In the form of the carapace *Microbrachius* resembles *Bothriolepis*, but the arms are short and the mode of articulation of the anterior dorso-median plate is altogether peculiar. Only the type species, *Microbrachius Dickii*, Peach sp., is known.

I have no material at present to enable me to enter into the discussion of *Actinolepis*, Ag., or *Chelyophorus*, Ag., of which the former at least is pretty certainly Asterolepid, as already noticed by Miller and Egerton; and the discussion of the general affinities of the group will form the subject of a subsequent communication.

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EXPLANATION OF THE PLATES.

(In all the figures the same letters refer to the same things.)

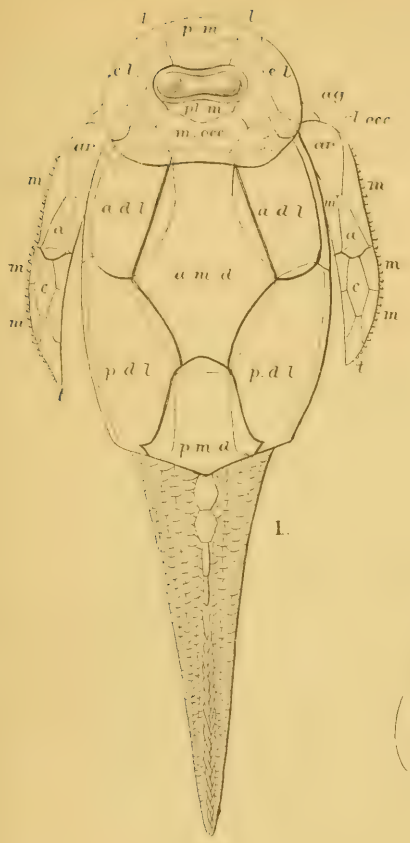
m. occ. Median occipital.
l. occ. Lateral occipital.
ag. Angular.
pt. m. Postmedian.
p. m. Premedian.
l. Lateral.
e. l. Extra-lateral.
mn. Mental plates, the "Unterkiefer" of Pander.
s. l. Semilunar.
a. m. d. Anterior median dorsal.
p. m. d. Posterior median dorsal.
a. d. l. Anterior dorso-lateral.
p. d. l. Posterior dorso-lateral.
a. v. l. Anterior ventro-lateral.
p. v. l. Posterior ventro-lateral.
m. v. Median ventral.
ar. Articular of limb.
a. Anconeal of limb.
c. Central of limb.
m. Marginal of limb.

Plate XVII.

Fig. 1. Restored outline of *Pterichthys cornutus*, Ag., seen from the dorsal surface. The thin black lines in this and figs. 2 and 3 denote the edges of the plates which are overlapped, and therefore concealed; the double dotted lines indicate the grooves occupied by the lateral canal-system.
Fig. 2. Restored outline of the same species seen from the ventral aspect.
Fig. 3. Restored outline of the same species, lateral aspect.
Fig. 4. Outline of extra-lateral plate of *Pterichthys*, natural size.

Plate XVIII.

Fig. 1. Outline of external surface of anterior median dorsal plate of *Asterolepis maximus*, Ag. sp., much reduced. The shaded area *z* is that overlapped by the front of the posterior median dorsal plate.
Fig. 2. Outline of the internal surface of the same plate; *x* and *y*, marginal areas overlapping the anterior and posterior dorso-lateral plates respectively.
Fig. 3. Outline of internal surface of anterior median dorsal plate of *Bothriolepis giganteus*, Traq.; *x*, area overlapping the anterior dorso-lateral.
Fig. 4. Restored outline of the dorsal aspect of *Bothriolepis hydrophilus*, Ag. sp., from specimens in the Edinburgh Museum. The overlapped edges of the plates are not given here, but the lateral-line grooves are shown by double dotted lines.
Fig. 5. Front of anterior ventro-lateral plates of *B. hydrophilus*; *s. l.*, the single plate representing the semilunars.
Fig. 6. Outlines of the bones of the head of *B. canadensis*, Whiteaves, from specimens in the Edinburgh Museum, except the plates filling the median opening, which are copied from Whiteaves.
Fig. 7. Anterior median dorsal plate of *Microbrachius Dickii*, Peach, sp., showing its articulation with the anterior dorso-laterals.
Fig. 8. Dorsal plates of the carapace of *Microbrachius Dickii* seen from the internal aspect; the outlines of the head and of one of the arms are likewise shown.



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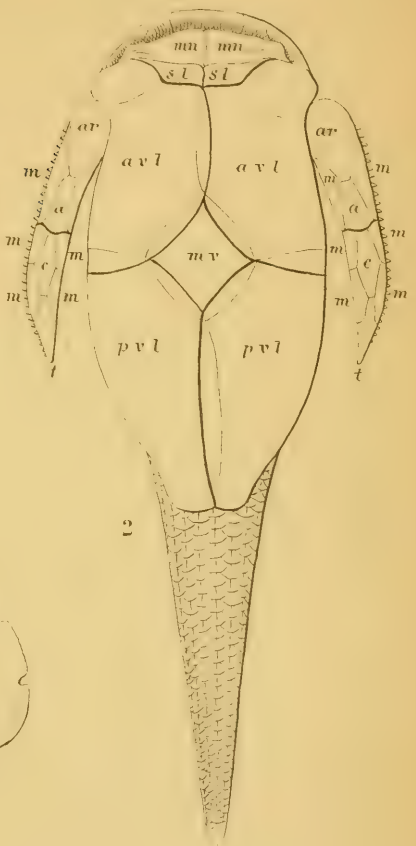

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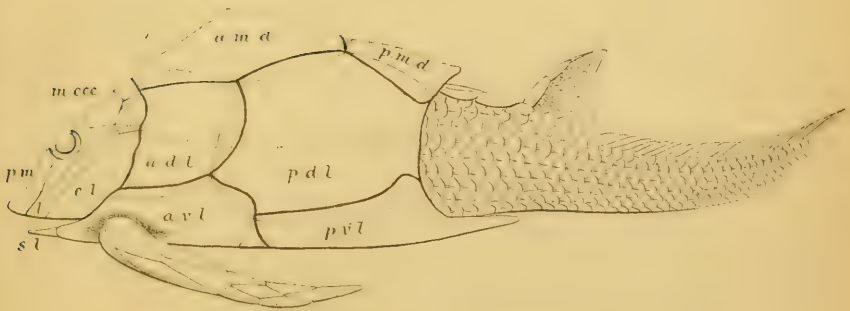

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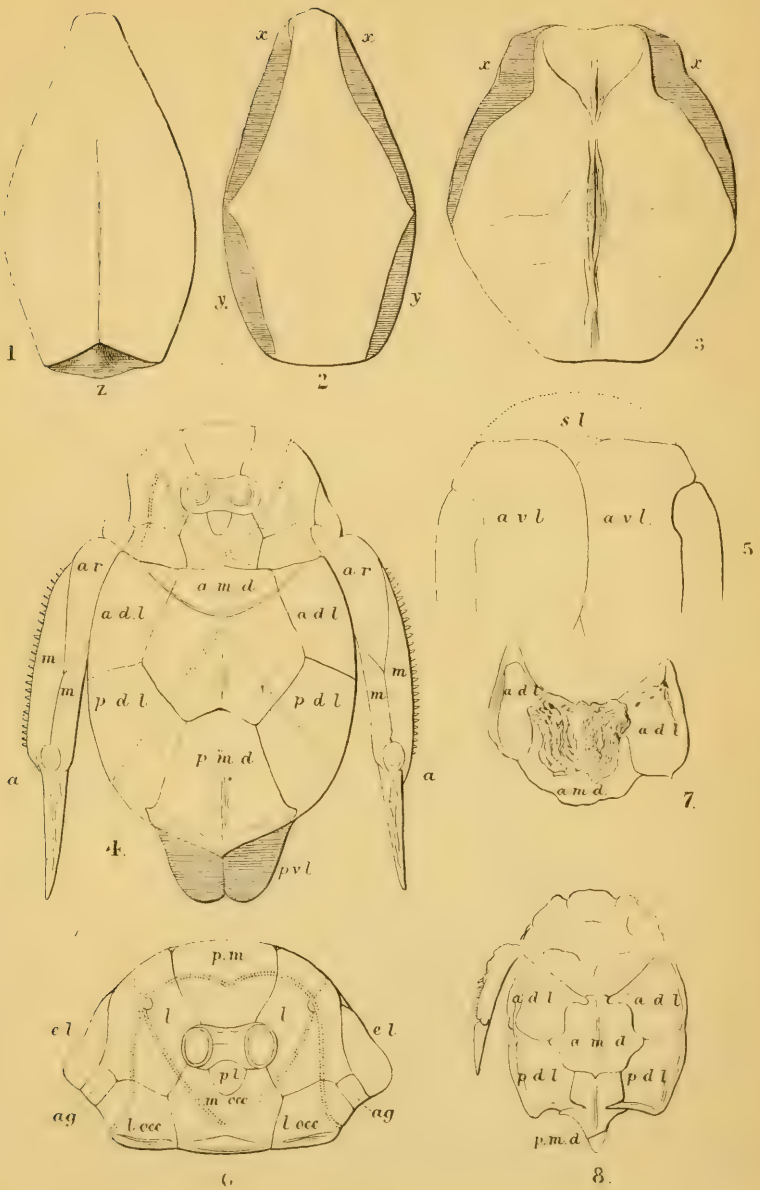

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